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ECOSYSTEM BEHAVIOR UNDER STRESS

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In his address to the 1st International Congress of Ecology, Margalef (1975, p. 239) suggested that "All or most of the ways in which man interferes with the rest of nature produce coincident or parallel effects. [For example] diversity is reduced, horizontal transportation [of nutrients] is increased and the ratio of production/biomass is increased. . . . The parallelism of change and its logical coherence represents a welcome simplification of the whole set of problems." While ecologists have sought to elucidate the nature of these "parallel effects" of stress on ecosystems (e.g., Woodwell 1967, 1970; Regier and Cowell 1972; Margalef 1975; Lugo 1978; Vogel 1980), they have perhaps more often followed what Dyson (1981) has identified as the predominant methodology of the biological sciences: a preoccupation with description of the diversity of phenomena, by and large to the exclusion of consideration of unifying themes.

The concentration of effort on documenting diversity particularly characterizes the field of "stress ecology" (Barrett et al. 1976). Its subject matter, the transformation of natural ecosystems by human activities, is rather wide ranging, encompassing all manner of ecosystems in association with the various kinds of stresses stemming from human activity. Numerous case studies have now yielded an extensive data base from which general features of ecosystem response to stress may be inferred.

In an attempt to bring some measure of coherence to otherwise diffuse and unrelated observations on ecosystem response to stress, we follow the physiologist, the late Hans Selye (1973, 1974), who provided a framework for stress physiology by identifying common symptoms of stress (in mammalian systems) and the phases of adaptation to stress. That Selye's framework has yet to find extensive application at the ecosystem level is, perhaps, because of the reluctance of ecologists to give much credence to a literal analogy of "ecosystem as organism." Ecosystems are, to be sure, a supraorganismic level of organization, but are

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not superorganisms since each level in a hierarchy has both unique properties found only at that level, and parallel properties with other levels. Accordingly, ecosystems are not organisms, but there are analogous properties that may or may not function in the same manner at the two levels (Knight and Swaney 1981). Since ecosystems in common with organisms are cybernetic (but not necessarily by the same mechanisms), and thereby have the potential to mitigate many stressors imposed from the outside, Selye's organism-level approach may have a valid parallel at the ecosystem level.

A difficulty in adapting Selye's approach to the ecosystem level is the variety of definitions given to basic stress concepts. Although more than three decades have passed since Selye first introduced unifying concepts of the effects of stress at the physiological level, usage of the various terms is not yet consistent. Selye learned that physicists used the term "stress" for the *applied stimulus*, but persisted in using it to connote the *response of the system*, with the term "stressor" referring to the stimulus. Ecologists have wavered in their definition of stress concepts. Thus we find that Odum et al. (1979) refer to the deviation or displacement of the ecosystem from the nominal state as "stress," while Barrett et al. (1976) refer to the same concept as the "response." Despite these differences, it seems clear that "All definitions of stress, however, share the common premise of a stimulus acting on a biological system and the subsequent reaction of the system" (Pickering 1981, p. 1).

In this paper we use "stress" to denote an external force or factor, or stimulus that causes changes in the ecosystem, or causes the ecosystem to respond, or entrains ecosystemic dysfunctions that may exhibit symptoms. Our use of "stress" is thus like Selye's use of "stressor"; ours is consistent with usage in the physical sciences generally. We have chosen not to use the physicists' term "strain" for an effect of a stress on a system, because it is not commonly used in the ecological sciences. Instead, we prefer "response" though we may also use perturbation, dysfunction, distress syndrome, etc., as approximate equivalents. Thus, for us a *stress* is usually an external cause and a *response* is usually an internal effect.

Not all stresses threaten the continued viability of ecosystems. Indeed, many ecosystems, as Vogal (1980) extensively documents, depend on a type of stress for their persistence. These events upon "which organisms and systems are dependent . . . are repetitive . . . (and) become expected or anticipated events that are part of natural systems" (p. 87). In contrast, Vogal elsewhere states, "general perturbations and stress usually create instability, reduce species diversity, set back the successional development, produce declines in productivity, cause degradation of the system or result in abrupt changes in the organisms or systems" (p. 87).

Events of the first type, the so-called "eustresses" (Selye's terminology), include phenomena such as the annual scouring of streambeds by spring runoff, periodic wind-induced "bands of death" in mature high-altitude balsam fir forests (Sprugel and Bormann 1981), wave-shearing action in the intertidal community (Paine 1979), and fire in the boreal forest.

Fire, for example, is now recognized as an essential component of a healthy

boreal forest. Some species depend upon fire for seed release from cones and have numerous adaptations which ensure their postfire survival. Periodic burns release minerals stored in the soils and in tree biomass, create space, and reduce competition for moisture, nutrients, heat, and light. Thus, young stands that are reestablished following such fires are less susceptible to attack by insects and diseases. This "sanitizing" or "immunizing" effect is particularly effective against spruce budworm, bark beetle (in lodgepole pine), and dwarf mistletoe (Heinselman 1971).

Events of the second type, on the other hand, serve to degrade and transform the ecosystem. Examples are all too plentiful: impacts from human activities, such as smelter emissions (Gorham and Gordon 1960; Hutchinson and Whitby 1974); smog (Williams 1980); oxidants (Westman 1979); coal surface-mining (Riley 1977); and catastrophic natural events, such as the recent eruption of Mount St. Helens (Wissmar et al. 1982). To this we might add the catastrophic effects of human conflicts and wars (Peterson 1982).

Our primary focus is empirical rather than theoretical. Much work of a theoretical nature on the properties of stressed ecosystems has been done and has contributed to the synthesis developed in the current work. Some representative works of this nature include Holling (1973), Orians (1975), Westman (1978), Odum et al. (1979), and O'Neill and Reichle (1980).

Drawing from representative empirical studies about the impacts of various stresses on the structure and function of aquatic and terrestrial ecosystems, we identify common symptoms of ecosystem distress and the major phases of ecosystem response to stress. We find that Selye's model (1974) serves to provide a unifying framework for the description of ecosystem behavior under stress.

SYMPTOMS OF ECOSYSTEM DISTRESS

In ecosystems as in organisms, what constitutes health is not (despite the popular view) based on objective scientific criteria, but rather involves judgment. Though recognition of ecosystem responses to distress involves objective comparison with a normal state, judgment enters in deciding which parameters are significant from this point of view. For example, from the perspective of trophodynamics studies, rates of nutrient cycling and primary productivity are of critical importance (O'Neill and Reichle 1980). In this context an ecosystem would appear unchanged if nutrient cycling and productivity remain relatively unaffected, even though species composition had changed considerably. In a grassland ecosystem, for example, primary productivity may remain more or less constant from year to year, while species composition fluctuates (McNaughton 1977). From the perspective of resource managers or naturalists, however, the species composition is of fundamental importance. Naturalists may value wetlands for their floristic diversity or for the presence of a rare plant species. Resource managers may value them because they provide breeding grounds for one or more species of waterfowl. The loss of one or more of such valued species would be considered a major degradation.

The signs or symptoms of ecosystem distress are thus, to a greater or lesser degree, dependent on one's perspective. In table 1, some representative case

TABLE 1

SYMPTOMS OF ECOSYSTEM DISTRESS

TYPE OF STRESS	RESPONSE VARIABLE					SOURCE
	Nutrient Pool in System	Primary Productivity	Size Distribution	Species Diversity	System Retrogression†	
Harvesting of renewable resources						
Opportunistic fishing	*	*	—	—	+	Regier & Loftus 1972
Commercial fishery: Great Slave Lake	*	*	—	—	*	Keleher 1972
Deforestation; northern hardwoods‡	—	—	—	—	+	Likens et al. 1978
Pollutant discharges						
Radiation; oak-pine forest	*	*	—	—	+	Woodwell 1967
Nutrient; lakes	+	+	—	*	+	Colby et al. 1972
Toxins; river	+	*	—	—	+	Cairns & Dickson 1977
SO ₂ ; boreal forest	—	—§	—	—	+	Gorham & Gordon 1960
SO ₂ ; coniferous forest, Poland	*	—	—	—	+	Wolak 1979
Oxidants; forest, San Bernardino Mts., Calif.	*	—	—	—	+	Miller et al. 1963; Miller 1973
Arsenic; boreal forest, Yellowknife, N.W.T.	*	—	—	—	+	Hutchinson et al. 1982
General air pollution; Central European forests	—	—	*	—	+	Ulrich et al. 1980
Physical restructuring by humans						
Coal surface mining; Ohio	—	—	—	—	+	Riley 1977
Shoreworks; Italian subalpine lakes	*	*	—	—	+	Grimaldi & Numann 1972
Toxic mine tailings; N.W.T., Yukon	—	—	—	—	+	Kuja & Hutchinson 1979
Pipeline construction; Arctic	+	—	—	—	+	Van Cleve 1972
China clay waste; Cornwall, U.K.	—	—	*	—	+	Bradshaw et al. 1975
Introductions of exotics; fish species	*	*	—	*	+	Regier 1973
Extreme natural events						
Hurricane; coral reef	*	*	*	—	+	Woodley et al. 1981
Earthquake; tropical forest	*	—	—	—	+	Garwood et al. 1979
Multiple causes						
Baltic Sea	+	+	*	*	+	Leppakoski 1980
Great Lakes	+	+	—	*	+	Regier & Hartman 1973

NOTE.—Signs (+ or —) indicate directions of change compared with normal functioning of relatively unstressed systems.

* Response was not monitored.

† The symbol + indicates that retrogression has occurred.

‡ Although the Hubbard Brook clear-cut was not designed to simulate a commercial harvest of the forest, "it soon became apparent that the results could provide significant insights into environmental questions posed by commercial cuttings in northern hardwood forests" (see Likens et al. 1978, p. 492).

§ Inferred from decrease in vegetation cover and nutrient pools.

|| Possibly acid rain; major effects noted so far are on spruce and beech.

studies have been tabulated in terms of both the primary stress (i.e., the agent inducing stress) and some commonly observed ecosystem manifestations of response to stress. The table is meant only to be illustrative, since very many other examples could equally be quoted.

In classifying stresses we have been pragmatic, reflecting conventional approaches to environmental problems (Francis et al. 1979; Rapport and Regier 1980). Five groups of stresses appear sufficient to include most of the specific impacts of human activity on natural ecosystems, as well as extreme natural events. (1) Harvesting of renewable resources directly affects the biotic capital of the ecosystem. (2) Pollutant discharges are purposely or accidentally made into air, water, or land, and include a variety of pollutants such as PCB's, SO₂, pesticides, heavy metals, oil spills, and radiation, in addition to sewage. Leakage into the environment often occurs from transportation, consumption, and storage of products, as well as from their production. At a finer level, a distinction might be made between man-made toxic substances (to which organisms have no adaptive evolutionary history) and excess organic matter (sewage) (Margalef 1981). (3) Physical restructuring includes purposive land-use changes, such as from forests to farms, wetlands to dry lands, sloping shores to harbors, lowlands to cities, valleys to artificial lakes, ridges to pits. (4) Introductions of exotics, both plant and animal, may be made intentionally or carelessly. (5) Extreme natural events occur with sufficient irregularity, such that they are not readily accommodated by the recipient ecosystem. Examples include volcanic eruptions, earthquakes, and climatic shifts producing prolonged droughts, etc. Human-caused disturbances of a totally devastating nature such as wars could be added here.

Recognizing that not all symptoms of ecosystem dysfunction occur or are detectable in every case, screening for damaged ecosystems might proceed parallel to medical practice, e.g., by monitoring a group of the most common indicators of ecosystem dysfunction. Odum and Cooley (1980) suggest establishing an ecosystem profile, consisting of a group of indicators for which there are established normal values. These values are, of course, often dependent on the age of the ecosystem. Just as medical practitioners routinely screen patients by examining a battery of physiological parameters (comparing these with age- and sex-dependent values), determination of ecosystem health generally requires screening for a group of indicators rather than reliance on a single indicator. It is recognized in both cases that the direction of deviation is less important than the magnitude. Some comment on the ubiquity of these signs and the various pathways involved in representative ecosystems follows.

1. Changes in nutrient cycling.—Downward leaching and lateral transport of nutrients is widespread in disturbed terrestrial and aquatic ecosystems. Clear-cutting of both temperate (Likens et al. 1978) and tropical (Smith 1981) forested ecosystems often results in significant losses of nutrients through leaching and soil erosion. The normal tight cycles of key nutrients become leaky. In the Hubbard Brook drainage system (Likens et al. 1978) nutrient losses following clear-cutting and suppression of revegetation by subsequent herbicide application are particularly well documented. Compared with an uncut mature forest, losses of nitrate nitrogen increased 10-fold, calcium 3-fold, and potassium 8-fold. These losses

represented between one-quarter and one-half of the total nutrient storage in biomass and organic matter.

The impact of air pollutants on forests also decreases nutrient availability, although different mechanisms are involved. For example, the deleterious impact of a lead smelter in southeast Missouri on a forested watershed (Jackson and Watson 1977) was mediated through disruption of decomposer activities (microarthropods particularly). This resulted in a decrease in nutrient cycling, leaching of nutrients in soils, and an accumulation of litter. Freedman and Hutchinson (1980*b*) reported similar results for nickel-copper pollution of a forest ecosystem at Sudbury, Ontario.

Nutrients leached from soils accumulate eventually in neighboring aquatic ecosystems (Hasler 1975). In Lake Erie, for example, the increase in the phosphorus concentration has been roughly proportional to the increased human population in the basin, and reflects, in addition to direct loadings of sewage, substantial inputs from nutrient runoff as a consequence of land-based activities (Francis et al. 1979).

2. *Changes in primary productivity.*—Changes in primary productivity often follow changes in nutrient availability. In Lake Erie the response to increased phosphorus loading was a tripling of the average algal biomass and an overall algal productivity increase of 20-fold because of increased spring and autumn production (Regier and Hartman 1973). Our designation of ecosystem dysfunction involves both untoward increases or decreases in productivity, since both signify fundamental changes.

Stresses other than eutrophication generally cause a decrease in primary productivity. In Jeffrey pine stands at lower elevations of Sequoia and Los Padres National Forests, premature needle die-off was attributed to oxidant air pollution (Williams 1980). In white pine stands in the eastern United States, chronic air pollution has reduced productivity through reduced foliar biomass, as evidenced by stunted needles and premature needle loss (Mann et al. 1980).

Natural stresses such as intense and chronic insect pressure also may affect primary productivity. One case (Morrow and LaMarche 1978) involves native Australian eucalyptus trees. Following insecticide treatments which reduced the grazing pressure of phytophagous insects, the annual growth rate of subalpine eucalyptus was considerably enhanced.

It may be that on theoretical grounds the ratio of productivity to biomass is a better response indicator than productivity alone, because productivity sometimes increases and sometimes decreases in response to stressors (as in the above examples; see tables 1, 2). The *P/B* ratio, however, almost always increases (Margalef 1975). In the present work we retain the simpler notion of productivity since few studies that we have seen provide data to examine the *P/B* ratio and its change under stress.

3. *Changes in species diversity.*—One of the most widespread signs of ecosystem response to distress is a reduction in species diversity. Patrick (1967) documented this in her now-classical studies of the effect of pollutants on estuarine diatom communities. Similar results have been found in a wide variety of ecosystems affected by various stresses, such as SO₂ emissions, radiation exposure, etc.

TABLE 2
CHARACTERISTIC RESPONSE OF ECOSYSTEMS TO STRESS

	Nutrient Pool	Primary Produc- tivity	Species Diversity	Size Distri- bution	System Retro- gression
Harvesting of renewable resources					
Aquatic	*	*	—	—	+
Terrestrial	—	—	—	—	+
Pollutant discharges					
Aquatic	+	+	—	—	+
Terrestrial	—	—	—	—	+
Physical restructuring					
Aquatic	*	*	—	—	+
Terrestrial	—	—	—	—	+
Introduction of exotics					
Aquatic	*	*	*	—	+
Terrestrial	*	*	*	*	+
Extreme natural events					
Aquatic	*	*	—	—	+
Terrestrial	—	—	—	—	+

NOTE.—Signs (+ or —) indicate directions of change compared with normal functioning of relatively unstressed systems.

* Characteristic response not sufficiently determined.

(Woodwell 1970; Gorham and Gordon 1960; Freedman and Hutchinson 1980a). The few exceptions to this general tendency are usually found when the stress results in a type of physical restructuring which increases habitat diversity. In the Finnish countryside, avian species diversity was higher in those rural areas with some settlement activity than in the uninhabited surrounding forests (Nuorteva 1971). In areas where silvicultural practices such as strip clear-cutting have taken place, bird abundance and diversity were greater than in uncut control plots (Crawford and Titterton 1979).

Moore (1983) pointed to findings that suggest that stress, if not too severe, serves to increase diversity. As an example, Moore cited the action of “keystone species” in preventing their prey from dominating an ecosystem through disproportionate commandeering of resources. Stresses of this type are internal rather than external to the system and akin to eustress, that is, the system is well adapted to and indeed dependent on the stress.

4. *Retrogression*.—It is hardly surprising that stress on natural ecosystems tends to shift species composition in favor of those species best adapted to new and harsher environmental conditions. In general, exotics or locally rare species tend to displace native abundant species and the invaders are more opportunistic in character and tend to be shorter-lived. In this sense, stress alters the character of a community in the direction of less mature systems. Thus, a kind of “retrogression” occurs, that is, an apparent reversion to an earlier stage of the successional process, e.g., the spread of the herb *Artemisia tilesii* at the SO₂-fumigated area of the Smoking Hills (Northwest Territories, Canada; Hutchinson et al.

1978). Woodwell (1967, p. 463), with reference to pollutant stressors acting on terrestrial ecosystems, observes that changes in the environment, whether brought about by "sudden changes in climate or catastrophically by fire or windstorm or even by fallout from a bomb, . . . tend to be just the reverse of those occurring during a normal succession: the communities are simplified, niches are opened, the nutrient inventory accumulated during succession is lost at least partially, the community becomes less stable, and a new succession begins, possibly marked by large fluctuations in populations that reproduce rapidly (such as insects) and can exploit the open niches."

Retrogression refers to the reversal of autogenic succession (Margalef 1975). It is documented for terrestrial ecosystems in the aftermath of disturbances such as fire, physical restructuring, and pollutant discharges, and for aquatic ecosystems in the aftermath of disturbances such as damming of a river (Isom 1971), nutrient loading, and various other stresses (Francis et al. 1979).

There has been much confusion about whether eutrophication of aquatic systems from cultural loading of nutrients fosters or hinders natural succession. The confusion seems to stem from a common coincidence of increased cultural loading of both nutrients and sediments. Sediment loading causes lakes to fill in faster than normal and thus leads to premature aging and death as it becomes transformed into land. The shallower a lake, the more effectively a given level of nutrient loading will cause eutrophication (Vollenweider 1968). Filling in of a lake with sediments thus causes simultaneous geomorphological senescence and ecological juvenescence or retrogression. In aquatic systems, oligotrophication is the term sometimes applied to the natural process of ecological succession, i.e., homologous to ecological succession on land following a forest fire or cessation of cultivation of a field.

5. *Changes in size distribution of species.*—A general effect of stress on both terrestrial and aquatic ecosystems is a reduction in the average size of dominant biota, at least temporarily. Woodwell's study (1967) of the effects of experimental irradiation on a forest ecosystem clearly shows reduced size in dominant vegetation. In this case, a single source of radiation was suspended several meters above ground in the middle of a late successional oak-pine forest. After 6 mo, five well-delineated vegetation zones were apparent. In the central area (in which exposures exceeded 200 R per day) only mosses and lichens survived. Surrounding this was a zone consisting mainly of sedges and a few sprouts of a heath-shrub layer. A third more distant zone consisted mainly of shrubs. A fourth zone contained oak trees, but no pine, and the fifth zone (farthest from the radiation source) had the original oak-pine community still intact. Exposures in this least damaged zone were less than 2 R per day.

Chronic air pollution, such as SO₂ discharges from a smelter on the boreal forest (Freedman and Hutchinson 1980a, 1980b; Gorham and Gordon 1963), produces similar effects (Woodwell 1970). Gorham and Gordon's study (1963) of the impact of a smelter on the surrounding boreal forest showed clearly that the smaller vegetation (herbs) was more tolerant than the overstory (tree) species and that the conifers were especially sensitive. Some species (white pine) were eliminated as far as 26 km from the smelter discharge, and the entire overstory disappeared

within a radius of 4.6 km. Close to the smelter (1.6 km), only a few species of herbs survived.

Several mechanisms might account for reduced size of vegetation under stress. Woodwell (1967) suggests that the smaller vegetation has an advantage with respect to energy income and expenditures, leaving more surplus energy available for maintenance and repair. As the size of the plant increases, maintenance requirements increase faster than income (from photosynthesis), thus depleting energy available for repair. Alternatively, smaller vegetation may be better able to protect reproductive tissues, by virtue of the fact that these sensitive tissues are either below ground or close to ground level for many sedges and grasses. Raunkiaer (1910) suggested the importance of this meristem protection as a response to overall climate, especially cold. We suggest it for many other stresses including pollutants. Sedges and grasses readily recover from most "contact stresses" (e.g., air pollution, wind, fire) because their meristems are protected below ground, whereas shrubs and trees largely lack this ability because their apical buds are suspended as targets in the air.

Fauna, too, decrease in size with stress. For example, as a consequence of pollution, eutrophication, harvesting, and introduction of exotic species, there has been a marked decrease in the average size of fish in the Laurentian lower Great Lakes. Historically, perhaps 50% of the total biomass of all fish in these lakes was contributed by individuals in excess of 5 kg; today, the corresponding figure is less than 1 kg (Regier 1979). The fishery, once dominated by the larger, longer-lived benthic species (including sturgeon, lake whitefish, lake trout, walleye, northern pike), is now dominated by the relatively small, shorter-lived, nonnative species (primarily the offshore pelagics, e.g., alewife and rainbow smelt).

6. *Other signs of distress.*—Less well documented symptoms of ecosystem distress include alterations in disease incidence and changes in amplitude of fluctuations in component populations.

A good many studies have touched on changes in disease incidence with stress, one of the most-cited being the effect of oxidant pollution in rendering ponderosa pine more vulnerable to attack by bark beetle (Dahlsten and Rowney 1980). Whether disease incidence is promoted or retarded by stress depends, however, on whether the impact is more serious for the hosts or their parasites (predators). In forest ecosystems (Kozlowski 1980), fungal attacks are often reduced by air pollution since pollutants are often more toxic to the pathogen than to the host. In some instances, this depends on the timing of the stress with respect to the disease-vector life cycle.

The differential effects of acid rain on the incidence of tomato blight provide an example (Shriner and Cowling 1980). In the inoculum-dissemination stage, acid rain retards blight (for this reason acid buffer sprays are sometimes used to protect tomato plants from blight damage). At a later stage of the disease-vector life cycle, however, acid rain enhances blight by increasing penetrability of host tissue through its effect on erosion of the leaf-surface cuticle.

Disease incidence is also an indicator of stress on aquatic ecosystems. For example, insecticides have been implicated in increasing susceptibility of fish to infection (Larkin 1974, p. 57). In some Swiss lakes, Roth and Geiger (1972) noted

that cyprinids increased markedly in abundance as a consequence of one or more stresses related to harvesting (of more preferred species), to eutrophication, to modifications of in-flowing streams, etc. When cyprinid populations became dense, massive outbreaks of disease often occurred. These involved a number of different pathogenic bacteria, some of which survived for abnormally long periods in the more enriched parts of the aquatic environment.

The amplitude of fluctuations of populations within stressed ecosystems generally increases as a result of destabilization of population buffering mechanisms. In the Laurentian lower Great Lakes fishery, eutrophication and opportunistic fishing contributed to increasingly erratic fluctuations in the commercial catch of long-lived native species (Regier and Hartman 1973). Of course, to the extent that stress induces ecosystem retrogression, further instability arises from a shift in species dominance to favor opportunistic shorter-lived species.

Management strategies which are directed toward smoothing out marked oscillations in ecosystem behavior which are normal to the long-term maintenance of the system are themselves stressful. The exclusion of fire in the boreal forest provides a well-documented example (Heinselman 1971). In such cases, the applied stress temporarily may reduce fluctuations, but over the longer term probably will have catastrophic consequences.

AN ECOSYSTEM-LEVEL DISTRESS SYNDROME

The signs or symptoms of distressed ecosystems do not generally appear in isolation. Indeed, the postulate of a linked set of symptoms has been a recurring theme in ecological writings. Margalef (1975), for example, observes that signs of distress include reductions in species diversity, increases in nutrient leaching, and an increase in the ratio of productivity to biomass. Woodwell (1970, p. 249) remarks that the patterns produced by pollutants are similar for a number of ecosystems and are characterized especially by "simplification of the structure of both plant and animal communities, shifts in the ratio of gross production to total respiration, and loss of part or all of the inventory of nutrients." Structurally, the impact of pollution involves "a shift away from complex arrangements of specialized species toward the generalist; away from the forest, toward hardy shrubs and herbs; . . . away from diversity in birds, plants and fish toward monotony; away from tight nutrient cycles toward very loose ones with terrestrial systems becoming depleted, and with aquatic systems becoming overloaded; away from stability toward instability especially with regard to sizes of populations of small, rapidly reproducing organisms such as insects and rodents that compete with man" (Woodwell 1967, p. 432).

For aquatic ecosystems, Regier and Cowell (1972) suggest that stress, whether it occurs as fishing exploitation, toxic waste disposal, dumping of nontoxic organic wastes and nutrients, or nutrient enrichment, usually produces similar ecosystem effects. Stress is manifest by reductions in the stability and diversity of aquatic ecosystems, elimination of the longer-lived, larger species, and a tendency to favor short-lived opportunistic species. The latter tendency is especially pro-

nounced with eutrophication. Thus at the ecosystem level, one can draw an analogy (Rapport et al. 1981) to what Selye (1975) has termed the "biological distress syndrome."

There are, however, important differences in the mechanisms related to distress at ecosystem and physiological levels. At the physiological level, the common responses of mammalian systems to a variety of stresses reflects "emotional arousal or awareness" to them (Pickering 1981, p. 3). No obvious parallel mechanism exists in ecosystems. Ecosystems, so far as we know, do not feel pain. At the ecosystem level, the remarkable parallelism or coincident effects in ecosystem response to stress (Margalef 1975) are not ascribable to a single mechanism, except perhaps in the context of Margalef's "information" conceptualization.

We make several observations with respect to the appearance of the general distress syndrome. First, seldom do all symptoms occur immediately. Usually there is a progression which might, in some cases, offer a limited diagnostic potential. For example, air pollution effects on forested ecosystems (from SO₂ emissions) may be observed first in losses of soil nutrients accompanied by accumulation of leaf litter caused by reduced microbial activity. These initial symptoms may be followed by a reduction in primary productivity, increased tree mortality (as a result of insect attacks), and finally a shift in species composition, involving the invasion of smaller, shorter-lived, exotic species (O'Neill and Reichle 1980; Kozlowski 1980). Bormann (1983) perceives a somewhat similar pattern of decline of the forest ecosystem under increasingly severe air pollution stress. In the earliest stages, the life cycle of sensitive species may be affected with detectable changes in reproductive success and predisposition to insect and fungus attacks. This change may also be reflected in reduced photosynthesis and deleterious effects on nutrient cycling. As pollution stress increases, sensitive species decline. With still more pollution stress, the community structure is drastically altered. At this stage, the large plant forms give way to the smaller forms, resulting in the marked size-structure changes observed by Gordon and Gorham (1963) and Woodwell (1970).

This sequence involving changes in reproductive success, followed by loss of sensitive species, and finally change in size structure is also characteristic of aquatic ecosystem response to some stresses, e.g., acidification. Here the sequence of symptoms typically involves a reduction of zooplanktonic, crustacean species, and benthic molluscs; followed by a lack of young fish because of failure to reproduce; followed by species changes in fish populations concomitant with changes in the phytoplankton species, including loss of blue-green algae and changes in diatom species; followed by extinction of all crustaceans and fish, and the predominant spread of benthic algae, sphagnum and other mosses, and liverworts.

Second, there is an evident linkage among features of distressed ecosystem. As shown in table 2, changes in primary productivity are linked with changes in nutrient availability (e.g., both indicators move in the same direction). Changes in species diversity, size distribution, and the retrogression of the system are also closely correlated.

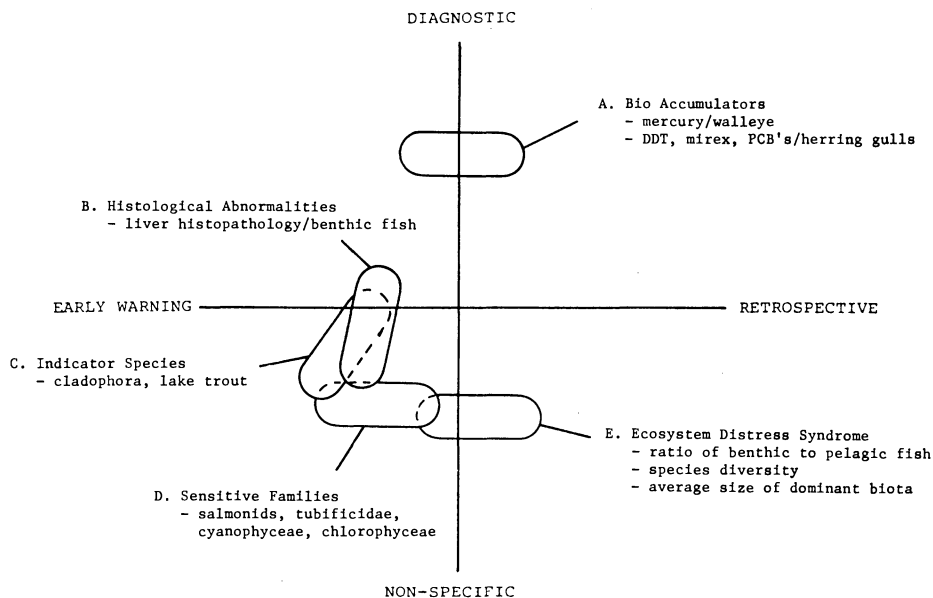


FIG. 1.—Indicators of ecosystem dysfunction. These 5 classes of indicators are commonly used to signal environmental change. Examples are taken from the history of transformation of Lake Erie. Virtually no group has the advantage of being both early warning and diagnostic. The assertion of causality between histopathology and environmental stress for field situations remains somewhat speculative.

Third, symptoms of ecosystem distress are, for the most part, retrospective. In this sense they are akin to “vital signs” in medicine, for changes in these are not usually manifest until the disease process is somewhat advanced.

Fewer prospective indicators of stress at the ecosystem level have been suggested, compared with numerous signs found at the biochemical and histological levels. In figure 1, we distinguish five classes of environmental indicators based on diagnostic and “early-warning” capability. Few indicators are both early-warning and diagnostic, particularly at the ecosystem level, though it can be argued that the decline in vigor, followed by the demise of particular lichen species in response to air pollution by fluorides or sulphur dioxide, may herald more general and widespread problems for less susceptible species (Hawksworth and Rose 1976).

AN ECOSYSTEM GENERAL-ADAPTATION SYNDROME

Recognizing that the appearance of an ecosystem distress syndrome often reflects an advanced stage of ecosystem response to stress prompts us to raise the question, What are the earlier stages in this process?

Here again Selye's model provides a parallel. Selye (1974, p. 39) described three stages in mammalian system responses to stressors: an alarm reaction in which

the body shows “changes characteristic of the first exposure to a stressor”; a “coping reaction” or “resistance stage” during which the “signs characteristic of the alarm reaction have virtually disappeared and resistance rises above normal”; and an “exhaustion” phase in which “the body adaptation energy is virtually exhausted, signs of disturbance again reappear, and unable to cope, death results.” Selye attributes this outcome to some “fundamental failure in the vitalization process.”

In their review of stress and cancer, Sklar and Anisman (1981, p. 369) refine to some extent the Selye paradigm. They comment, “The initial physiological reaction to a stressor is believed to reflect adaptive changes to meet environmental demands. With further stress, additional compensatory changes may also occur, again in an attempt to meet the environmental demands placed on the organism. If the stressor is sufficiently severe, continuous and protracted, the physiological coping mechanisms may not be capable of preventing the eventual demise of the organism. Behavioral coping is considered to be those responses that (a) reduce the exposure of the organism to the stressor and (b) reduce the physiological consequences of exposure to stressors that are otherwise observed.”

Ecosystem equivalents to Selye’s concepts of “alarm reactions, coping mechanisms, and succumbing” may be found in a number of case studies. This gives rise to a sequence of events in which it may be possible to observe (1) initial effects of a stress (equivalent to Selye’s “alarm reaction”); (2) feedback mechanisms that are called into play at the ecosystem level to mitigate the effect of stress (the “coping” reaction); and (3) in those cases in which these responses are inadequate, the transformation, or breakdown of the ecosystem, or in Holling’s terms (1973), the “flip” of the system to another “domain of attraction.”

Alarm reactions.—The earliest indications of ecosystem response to stress may be found in abnormal fluctuations in sensitive populations or communities, abnormalities in reproduction, changes in the distribution of sensitive species, and in the case of contaminant stress, biochemical or histological abnormalities within populations and organisms. Such early-warning symptoms manifest themselves primarily at the reproductive and species-specific levels. Examples abound. The disappearance or alteration in the species composition and size spectrum in lichens may serve as an early-warning indicator of chronic air pollution in forested ecosystems (Hawthornthwaite and Rose 1976). Failures in reproduction of herring gulls (Peakall 1970) revealed the serious impacts of DDT and other toxic substances in the Laurentian lower Great Lakes. On the California coast, brown pelicans ceased breeding and raising healthy young in the early 1970s, while there remained thousands of apparently healthy adults. This failure to reproduce was linked to the presence of chlorinated hydrocarbon pesticides from inland agriculture (Schreiber 1980). Char and closely related fish species (lake trout, herring, whitefish) are more sensitive to nutrient, toxic, and harvesting stresses than most fish species; thus, a “salmonid watch” has been proposed as an early-warning detection of threats to northern Canadian aquatic ecosystems (Maitland et al. 1981). Tubificids have long been recognized as sensitive biological indicators of adverse nutrient and toxic conditions in aquatic ecosystems (Brinkhurst 1966), and the composition of the tubificid community, as well as their absolute abun-

dance, is highly correlated with stress intensity from urbanization on the shores of Lake Ontario (N. A. Thomas and W. A. Christie, MS).

More rarely, ecosystem-level effects are detectable prior to changes in species or populations. For example, the impact of a lead smelter on a southeastern Missouri forested ecosystem (Jackson and Watson 1977) was first detectable by the accumulation of litter which suggests impaired decomposer activity. In a study of the effects of toxic substances on terrestrial ecosystems, O'Neill et al. (1977) reported that the first signs of disturbance were detectable in increased nutrient leaching, well before any change in population or community parameters was noted. This is now also occurring in areas subject to acid rain, with accelerated leaching of foliar and soil calcium and magnesium.

Some biochemical early-warning indicators of stress that function primarily at the organismal level might also apply at the ecosystem level. One suggestion along these lines is adenylate energy charge ratios. The charge ratio based on the cellular adenine concentrations (ATP, ADP, and AMP) has been proposed as a measure of the energetic state of microbial populations in vivo (Witzel 1979). The ratio is defined by the molar concentrations of adenine nucleotides: more specifically, $(\text{ATP} + \frac{1}{2} \text{ADP}) : (\text{ATP} + \text{ADP} + \text{AMP})$ (Atkinson and Walton 1967). This ratio (which ranges theoretically between 0 and 1) declines for microbial population under starvation. If this proves to be an early-warning indicator of community or ecosystem distress, then this might be analogous to the change in adrenal hormone output in Selye's "alarm" stage.

Coping mechanisms.—While ecologists still debate the point (McNaughton and Coughenour 1981), it seems clear that ecosystems have cybernetic mechanisms which operate to counteract the impact of stressors, at least to some extent. These mechanisms may be chemical or biological in nature and in certain instances entail deactivation of the stressor itself.

The ecosystem's ability to cope with specific stresses appears, in part, to be a function of its evolutionary history. Ecosystems which have evolved in relatively unstable environments are more likely to resist moderate stresses from human activity, especially those which mimic natural stresses. Thus boreal forest vegetation which is subject to periodic burning might be able to cope with stresses such as SO₂ which in its phytotoxic effect simulates aboveground defoliation by burning. Some examples of preadaptation of ecosystems to stress are given in table 3.

Margalef (1975, p. 241) suggests that "Ecosystems that never have gone through the selection of serious environmental stress, such as tropical forests, coral reefs and oligotrophic lakes will be the first to go," whereas naturally stressed ecosystems "are more resilient to increased stress and can absorb more disturbance due to increased stress—short of final catastrophe." Holling (1978, p. 34) holds a similar view: "Natural systems are . . . continually being 'tested,' and their adaptation to that experience affects their response to new intrusions. Some paleoecologists have suggested that the species complex within intertidal communities has changed less than that in deeper water communities. The former are exposed to continual extremes through tidal movement; the latter experience a much less variable world because of stabilizing properties of water. Hence, when the inevitable unexpected occurs, the intertidal species can adapt while the

TABLE 3
ECOSYSTEM PREADAPTATION TO STRESS

Ecosystem	Natural Stressor	Novel Stressor to Which System Preadapted	Mechanism of Preadaptation	Source
Boreal forest	Fire	SO ₂	Intercalary meristem & underground overwintering organ	Raunkiaer 1910
Estuary Tundra	Nutrient flux Extreme cold, short growing season	Industrial chemicals SO ₂ & oil spills	Cellular buffering Underground overwintering organs	Fisher 1977 Hutchinson 1981
Deciduous forest	Winter factors	Air pollutants occurring during winter episodes	Dormant period	
Prairies & deserts	Drought	SO ₂ & fluoride	Low metabolic rate, large no. annuals surviving by seed Grasses with intercalary meristem	

deepwater species cannot.” Fisher (1977) provides experimental evidence that algal species cloned from the Sargasso Sea (a relatively stable environment) were less resistant to novel chemical stresses (in the laboratory) than closely related species from estuarine clones. He suggests that “physiological adaptations of estuarine organisms to a particular set of pressures may enable them to tolerate a multitude of other stresses” (p. 891).

The precise mechanism whereby ecosystems resist or cope with stress varies. One mechanism involves the replacement of the more stress-sensitive species with functionally similar, but more resistant species. This “congeneric homeostasis” (Hill and Wiegert 1980) preserves overall functional properties of the ecosystem such as productivity and nutrient cycling. For example, in northern hardwood forests, resistance to effects of clear-cutting, in particular to the erosion of nutrient capital, involves recolonization by vegetation well adapted to conserve nutrients (Marks and Bormann 1972; Bormann et al. 1974). In this case, recolonizing pin cherry played a role in conserving nitrogen and calcium in the ecosystem. Nitrogen uptake by this species was one-third greater in the recolonized site than in the undisturbed ecosystem (Melillo and Bormann 1976).

Another mechanism involves external biogeochemical feedback loops. Margalef (1981, p. 286) describes the manner in which aquatic ecosystems resist eutrophication. “The characteristic response of ecosystems subjected to such forms of stress is the development of external loops, which lead outside the system of reference, through the atmosphere for the oxygen and nitrogen, and through the sediment for the carbon and phosphorus. Forcing a system (i.e., overfeeding it) means some extra input, and probably the use of some external energy, accelerating primary production and the general flow of matter per unit

area. Through the development of external loops, the system manages to counteract the imposed change, apparently obedient to the principle of Le Chatelier and Braun.”

In terrestrial ecosystems, chemical feedback involves the conversion of toxic compounds to less deleterious forms. Heavy metals are chelated in soil organic matter, and gaseous SO_2 is converted to sulphate. With acute stress the main mechanism of detoxification is dissipation and degradation. Both biological and nonbiological processes are involved. “Dissolution and diffusion expose the contaminants to photo-oxidation and other reactions energized by sunlight, while transport onto soil or mud leads to both surface catalyzed reactions and, especially, microbial degradation. . . . Perhaps the most important process of contaminant destruction is volatilization followed by photo-oxidation in the atmosphere” (Neuhold and Ruggerio 1975, p. 16).

Throughout the resistance phase, there may be an increase in community respiration which reflects the dissipation of energy to cope with stress (Lugo 1978). This constitutes a drain on the energy available to do useful work in the ecosystem and these changes in energy flows provide an indicator of stress (Odum 1967). Indexing the energy drain by the ratio of respiration to biomass yields an indicator of broad applicability since the changes in energy flows presumably are affected by many different types of stress. The community metabolism approach to stress is reviewed by Lugo (1978).

Ecosystem breakdown.—For any homeostatic system, homeostasis cannot be maintained indefinitely if stress is sufficiently prolonged or intense. For cases in which ecosystem breakdown occurs, the removal of the stress may no longer be sufficient to restore the system to its initial state.

Niering and Goodwin (1974) describe the effects of long-term herbicide spraying in a forested area. Once the spraying program was terminated, the shrub system did not revert back to forest. A similar phenomenon (O. Loucks, personal communication) has been observed in the eastern deciduous forests of Canada, where abandoned farmland remains in shrubs. In tropical areas, land clearing often has led to treeless areas and seemingly irreversible conditions, due in part to soil exhaustion from nutrient leaching (Smith 1981). The time scales being considered may be of fundamental importance in the above examples.

Ecosystems may become more vulnerable to transformation from a given stress if this occurs along with other stresses. The effects of sulphur dioxide on particular forest trees, such as white pine, very often appear to be exacerbated if elevated levels of ozone also occur (Costonis 1971). Frequently, air pollution damage to forests causes predisposition to injury or death by insects, especially bark beetles (Dahlsten and Rowney 1980). In aquatic systems, synergistic interactions between toxic metals have been described. In Sudbury area lakes, copper and nickel act synergistically on a number of algal species, whereas increasing calcium levels reduce the individual toxic effects (Hutchinson 1973). Similarly, copper-nickel synergism has also been described for the floating aquatic plants *Salvinia natans* and the duckweed *Lemna valdiviana* (Hutchinson and Czyrska 1972). In the severely stressed Green Bay of Lake Michigan, Harris et al. (1982) found that ecological synergism among different stresses was quite common, unfortunately.

Less often, stresses interact antagonistically. Where they do, vulnerability to transformation is reduced. One case involves copper toxicity from a nearby smelter (Whitby et al. 1976) mitigated by sewage inflow to an Ontario lake; the unexpectedly healthy and abundant photoplankton community in a lake with a heavy metal content was attributed to the mitigating effects of sewage inputs in which "Organic ligands complexing potentially-toxic heavy metals seem to be part of the answer . . ." (p. 56). Another case involves cadmium toxicity to various unicellular algal species mitigated by increasing concentration of selenium (Hutchinson 1973).

Repeated exposure to the same stress can cause "stress fatigue" leading to ecosystem breakdown. This has been shown in the field with experimentally introduced oilings of salt marsh plants, *Spartina anglica* (Baker 1971). With 8 successive oilings, the peak density of *Spartina* shoots was reduced to less than half those in the control plots. With 12 successive oilings, recovery was greatly delayed and the peak was reduced 10-fold (Baker 1971).

The historic recovery of an upland area in Northern Ireland after repeated episodes of land clearing also suggests the effects of stress fatigue. During the period 5000 B.C. to 1000 A.D., regeneration of the forest became progressively weaker and led to more open conditions. Similarly, in the Jutland heath in northern Germany, on base-poor soils "the successive waves of regrowth got progressively weaker until the forest ultimately failed to return" (Dimbleby 1978, p. 137).

One of the few empirical studies suggestive of all three phases of the ecosystem General Adaptation Syndrome is that of Whillans (1979). He describes (fig. 2) the phases of transformation in the nearshore fisheries of three representative bays in the Laurentian lower Great Lakes in the following terms: in the first phase (analogous to the "alarm reaction"), there were rapid increases in the cumulative recruitment of new species and in the total number of species fluctuating in abundance; in the second phase (coping), there was a leveling off of recruitment and a diminution in the number of fluctuating populations; in the final phase (succumbing), there was a rapid rise, once again, in the number of species drawn into the transformation. The correspondence of these events to Selye's General Adaptation Syndrome (fig. 3) is apparent.

While Whillans' study focuses on fish populations and thus is, strictly speaking, at the community level, the parameters of interest (e.g., species diversity and fluctuations) apply as well to the ecosystem level. A more convincing case might be made of historical transformation in the lower Great Lakes. Unfortunately, by the end of the 19th century the early phases of this transformation were well under way before monitoring fish communities and associated ecosystem parameters commenced.

AN APPLICATION TO ENVIRONMENTAL MANAGEMENT OF THE GREAT LAKES

A systematic approach to the rehabilitation of damaged ecosystems and the maintenance of ecosystem health requires an identification of the major effects or symptoms of stress, in order to judge the health of the environment. Recent

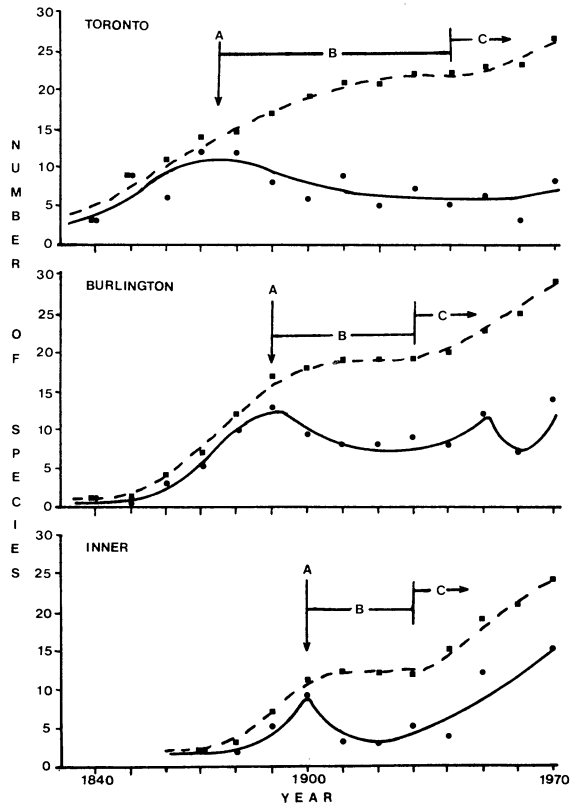


FIG. 2.—Historic transformation in 3 bays of the Laurentian lower Great Lakes. A, Stress peak; B, coping; C, intensifying stress. Solid curve is total number of species fluctuating in abundance. Dashed curve is cumulative recruitment of new species into the transformation. In the transformation of both systems, the initial symptoms of stress are reduced during the resistance or coping phase and reappear or intensify in the final phase. For the organism, the final transformation is to a decomposer system (death), whereas for the ecosystem, the transformation is to an alternative (degraded) state. Figure adapted from Whillans (1979).

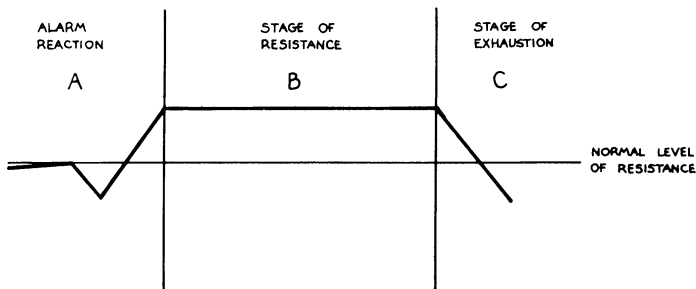


FIG. 3.—Three phases of the general-adaptation syndrome in organisms: A, alarm reaction; B, stage of resistance; C, stage of exhaustion. Figure redrawn from Selye (1974).

environmental legislation, international agreements and accords (e.g., the 1978 Water Quality Agreement between Canada and the United States) have come to recognize the importance of protecting the "integrity of ecosystems" and of maintaining "ecosystem health." It is thus a challenge to the scientific community to develop measures for assessing the quality of the natural environment.

The recognition of a general distress syndrome at the ecosystem level provides clues about appropriate indicators and at the same time suggests the difficulty in relating single indicators to specific stresses. In the Great Lakes some of the more stressed areas are the bays and streams where many man-made stresses have been operating, often intensely. These degraded subsystems exhibit the general distress syndrome. Because many of the stresses, if acting individually and to an extreme degree, elicit at least some of the features of the syndrome, "one-stress" experts have tended to ascribe primary causation to the particular stress that each understood well. This has led to one-stress management plans and interventions that often have not been effective, let alone efficient.

An appreciation of the fact that many factors, acting separately or jointly, could have a similar gross effect has led to an attempt to develop a practical approach from this perspective (Francis et al. 1979). Several bays of the Great Lakes, each of which was subject to a number of different man-made stresses, have now been studied. The types and approximate intensities of the mix of stresses could be inferred from an examination of the types of user groups that intervened ecologically in one system (Regier et al. 1980; Harris et al. 1982). The likely ecological responses, both specific and general, from each stress could be inferred from case studies related to impact assessment. From such beginnings, a fairly comprehensive and detailed interdisciplinary set of conceptual frameworks was developed, and now forms a basis for rehabilitation of the Great Lakes ecosystem (Francis et al. 1979). Appropriate information services are now being developed (Regier and Rapport 1983).

CONCLUDING STATEMENTS

Ecosystems exhibit considerable uniformity in their general response to various stresses. From an examination of a number of case studies involving various combinations of stresses acting on diverse ecosystems, a core set of ecosystem-level signs of distress can be identified. The ecosystem distress syndrome (analogous to what Selye has termed the "biological distress syndrome" at the organismic level) is largely nonspecific with respect to the causal agent.

Not all signs or symptoms of ecosystem response to distress appear at the onset of stress. Generally, there is a progression from symptoms specific to particular stresses (usually at the organism and population level) to less specific signs at the whole-ecosystem level. Ecosystems have a variety of homeostatic (or homeorhetic) mechanisms, which may, for a time, mitigate the effects of stress. Under prolonged, intensified, or repeated stress episodes, ecosystems eventually succumb.

Further understanding of the pattern of ecosystem transformation under stress is more likely to emerge from empirical studies at the whole ecosystem level than

from a priori theorizing at the population or community level. As is normally the case in good science, improved predictability of responses should follow empirical generalizations (Rigler 1982).

Analogy based on the work of Selye in conceptualizing stress effects at the physiological and organismic level has been used as a source of ideas to be tested empirically. In all of this, Selye's concepts have shown considerable potential at the ecosystem level. They also are contributing to the development of tools for the diagnosis and treatment of ecosystems under stress (Rapport et al. 1981).

SUMMARY

The behavior of ecosystems under stress can be shown to be analogous to Selye's characterization (1973, 1974) of the response of higher organisms to stress. The ecosystem-level distress syndrome is manifest through changes in nutrient cycling, productivity, the size of dominant species, species diversity, and a shift in species dominance to opportunistic shorter-lived forms. These symptoms of ecosystem dysfunction are common in both terrestrial and aquatic systems under various stress impacts including harvesting, physical restructuring, pollutant discharges, introductions of exotic species, and extreme natural events (such as disastrous storms or volcanic activity). The progression of appearance of symptoms under intensifying stress levels may be interrupted temporarily as ecosystem homeostasis and homeorhetic mechanisms intercede. Inability to cope leads to further dysfunctions and, perhaps, to irreversible ecosystem breakdown.

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